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SCANNING ELECTRON MICROSCOPIC STUDY OF NORTH AMERICAN *POGONOMYRMEX* (HYMENOPTERA: FORMICIDAE)[1]

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Abstract.—A SEM study of 16 *Pogonomyrmex* taxa from the U.S.A. is presented. Taxa representing both groups previously referred to as subgenera and all four complexes of the nominate subgenus are examined. Some previously used surface structure terminology is corrected for the genus and the head of a bilateral gynandromorph of *P. occidentalis* is illustrated. The problematic nature of *P. huachucanus* is discussed.

The ant genus *Pogonomyrmex* Mayr is confined to the New World and is represented in North America by 29 species (Cole, 1968; MacKay, 1980; Snelling, 1981a; MacKay et al., 1985). These ants are commonly known as "harvesters" because they store seeds within their nests, possibly as a food source. Most of these ants are xerophilous and only one species occurs east of the Mississippi River in the U.S.A. The greatest concentration of species in the U.S.A. is in the desert Southwest.

Pogonomyrmex are the dominant ant throughout much of their range. Damage to cultivated crops through seed harvesting, grass cutting, and construction of large, durable mounds adversely affects both the farmer and urban resident. These insects often build nests near the road shoulder where extensive tunneling causes the road surface to crumble and collapse, forming potholes. Medically, harvester ants are important because of their highly algogenic stings which cause anaphylactic shock in hypersensitive victims. These ants are also of taxonomic interest because of the poorly understood relationships between congeners.

Wheeler (1902) divided *Pogonomyrmex* into two subgenera, *Ephebomyrmex* Wheeler and the nominate subgenus, based on the heavier sculpturing, smaller size, and reduced psammophore of *Ephebomyrmex.*

The subgenera created by Wheeler were retained by Creighton (1950) in his key to the ants of North America. Creighton considered that the criteria chosen for the recognition of *Ephebomyrmex* were inappropriate and that the reproductive forms required further study. He noted that the thoraces of females of *P.* (*E.*) *imberbiculus* lack the elevated scutellum of *Pogonomyrmex* sens. str. (Creighton, 1956). Angular metasternal flanges and an irregular or absent row of gular hairs (ammochaetae) that form the psammophore distinguish *Ephe-*

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bomyrmex workers from those of the other subgenus in his key (Creighton, 1950).

Gallardo (1932) claimed that certain South American species of *Pogonomyrmex* had incomplete psammophores and that this condition was found in both subgenera. Although these species seemed to be clear examples of intermediate forms, Wheeler specified the absence of a psammophore as a distinguishing character between the two groups. Gallardo recommended that the subgeneric distinction be abandoned.

At the other extreme, an attempt to raise *Ephebomyrmex* to full generic status was made by Kusnezov. According to Kusnezov (1959), Wheeler distinguished the subgenus *Ephebomyrmex* on the basis of the following characteristics: (1) the absence of a psammophore, (2) a small head, (3) highly curved mandibles, and (4) heavy sculpturing on the head and thorax. Kusnezov (1949) agreed with the importance of the psammophore but argued that the sculpture, head size, and mandible differences were not acceptable characters for discrimination. He described *Ephebomyrmex* as the most primitive taxon within the genus, yet *Pogonomyrmex* sens. str. could not have evolved from these ants because there are secondary derivations in the wing venation of *Ephebomyrmex* males and females. In addition, maxillary palp conformation and the presence or absence of a psammophore were considered definitive generic differences (Kusnezov, 1959). Consequently, Kusnezov (1959) treated *Ephebomyrmex* and *Pogonomyrmex* as distinct genera in his key to the ants of Patagonia.

Snelling and George (1979) and Snelling (1981b) regarded *Ephebomyrmex* as a separate genus because its members possess poorly developed psammophores, matinal/crepuscular foraging habits, and are omnivorous. In the key to the desert ants of California (Snelling and George, 1979), *P. imberbiculus* is separated from the nominate subgenus by virtue of its distinctly off-center eye and a prominent ridge connecting the weakly developed epinotal spines. MacKay and MacKay (1984) and Wheeler and Wheeler (1985) recently concurred with the treatment of *Ephebomyrmex* as a separate genus.

The North American species of *Pogonomyrmex* were revised by Cole (1968), and this work is currently the standard reference. Cole divided the North American members of the genus into two subgenera, *Ephebomyrmex* Wheeler and the nominate subgenus. The latter group contained four complexes and 24 species, whereas *Ephebomyrmex* contained three species and was not subdivided into complexes.

Pogonomyrmex huachucanus Wheeler is presently considered a member of *Ephebomyrmex* and was described on the basis of workers only (Wheeler, 1914). Wheeler noted that the gular area enclosed by the psammophore and the sculpture of *P. huachucanus* suggest that this ant is "transitional between the species of *Pogonomyrmex* sens. str. and the subgenus *Ephebomyrmex* Wheeler." Nevertheless, Wheeler placed that species in the nominate subgenus. Creighton (1952) eventually described the reproductive forms of *P. huachucanus.*

Cole agreed with Wheeler's subgeneric concept and considered that the subgeneric distinction was upheld by certain "definitive characters" on the reproductive female thorax. Creighton (1956) first discovered these differences: The outline of the thorax was supposed to be smooth in *Ephebomyrmex* and disrupted in *Pogonomyrmex* sens. str. Although the illustration by Creighton suggests that *P. huachucanus* is allied with the nominate subgenus, the drawing by Cole (1968) indicates a closer affinity to *Ephebomyrmex.* One of the illustrations might be inaccurate or the character might be variable. A single reproductive female examined during the current study closely resembles Cole's figure.

The revision by Cole (1968) of *Pogonomyrmex* and all previous taxonomic descriptions were based upon external char-

acters only. Certain taxa were distinguished primarily on differences in surface detail, and scanning electron microscopy is ideally suited to reveal these differences. In an effort to better define some of these characters, an SEM study was undertaken.

Materials and Methods

Sixteen taxa, representing both subgenera of *Pogonomyrmex* and all four complexes of the nominate subgenus were available for study. The collection data, museum and figure numbers for these samples follow (TTU# = catalogue number of voucher series in the entomological collection of The Museum, Texas Tech University):

Subgenus *Pogonomyrmex* Mayr
badius complex
Pogonomyrmex badius (Latreille). Figs. 2–6; Florida: Leon Co., Tallahassee. 25 September 1985, TTU# 6957.
barbatus complex
Pogonomyrmex apache Wheeler. Figs. 11–12; Arizona: Yavapai Co., Clarksdale. 1 July 1985, TTU# 6831.
Pogonomyrmex barbatus (Smith). Figs. 13–16; Texas: Brazos Co., College Station. 2 June 1985, TTU# 6964.
Pogonomyrmex desertorum Wheeler. Figs. 7–10; Arizona: Cochise Co., 4.8 km E Portal. 20 June 1985, TTU# 6754.
Pogonomyrmex rugosus Emery. Figs. 17–20; Texas: Garza Co., 4.8 km E Southland. 27 August 1985, TTU# 6949.
maricopa complex
Pogonomyrmex californicus (Buckley). Figs. 41–45; California: Kern Co., Bakersfield. 28 June 1985, TTU# 6925.
Pogonomyrmex californicus [*estebanius* sensu Pergande]. Figs. 46–47; California: San Bernardino Co., 4.8 km E Apple Valley. 29 June 1985, TTU# 6802.
Pogonomyrmex comanche Wheeler. Figs. 1, 31–37; Texas: Houston Co., Grapeland. 24 September 1985, TTU# 6953.
Pogonomyrmex magnacanthus Cole. Figs. 48–49; California: Riverside Co., 1.6 km W Indio. 30 June 1985, TTU# 6825.
Pogonomyrmex maricopa Wheeler. Figs. 38–40; Texas: El Paso Co., 30.4 km E El Paso. 19 June 1985, TTU# 6746.
occidentalis complex
Pogonomyrmex brevispinosus Cole. Figs. 25–27; California: Kern Co., 17.6 km E Shafter. 28 June 1985, TTU# 6782.
Pogonomyrmex montanus MacKay. Figs. 28–30; California: San Bernardino Co., 9.6 km E Fawnskin. 29 June 1985, TTU# 6927.
Pogonomyrmex occidentalis (Cresson). Figs. 21–22; New Mexico: Grant Co., 17.6 km W Jct. US 180 & NM 78. 2 July 1985, TTU# 6834.
Pogonomyrmex subnitidus Emery. Figs. 23–24; California: Los Angeles Co., 8 km S Palmdale. 27 June 1985, TTU# 6763.
Subgenus *Ephebomyrmex* Wheeler
Pogonomyrmex huachucanus Wheeler. Figs. 55–58; Arizona: Cochise Co., Huachuca Mts., Miller Canyon. 21 June 1985, TTU# 6696.
Pogonomyrmex imberbiculus Wheeler. Figs. 50–54; Arizona: Cochise Co., 4.8 km E Portal. 20 June 1985, TTU# 6745.

The insects were preserved in 80% ethanol and were thoroughly dried before mounting. Representatives of the worker castes were fixed to aluminum stubs, coated with gold/palladium in a sputtering device, and placed in the vacuum chamber of the microscope. A Jeol JSM-25S scanning electron microscope and a Polaroid camera using Polaplan 4 × 5 Land Type 52 Film were used to photograph the ants. The head and thorax of each species were photographed, and additional distinctive or illustrative features were selected from certain taxa. The characters and general morphology (Fig. 1) discussed are those considered important in the revision of the genus (Cole, 1968). Terminology generally follows that used by Cole, but occasional use was made of works by Torre-Bueno (1962) and Harris (1979).

Results and Discussion

The sculpturing of the head and thorax as well as the appearance of the spaces between the rugae covering these structures

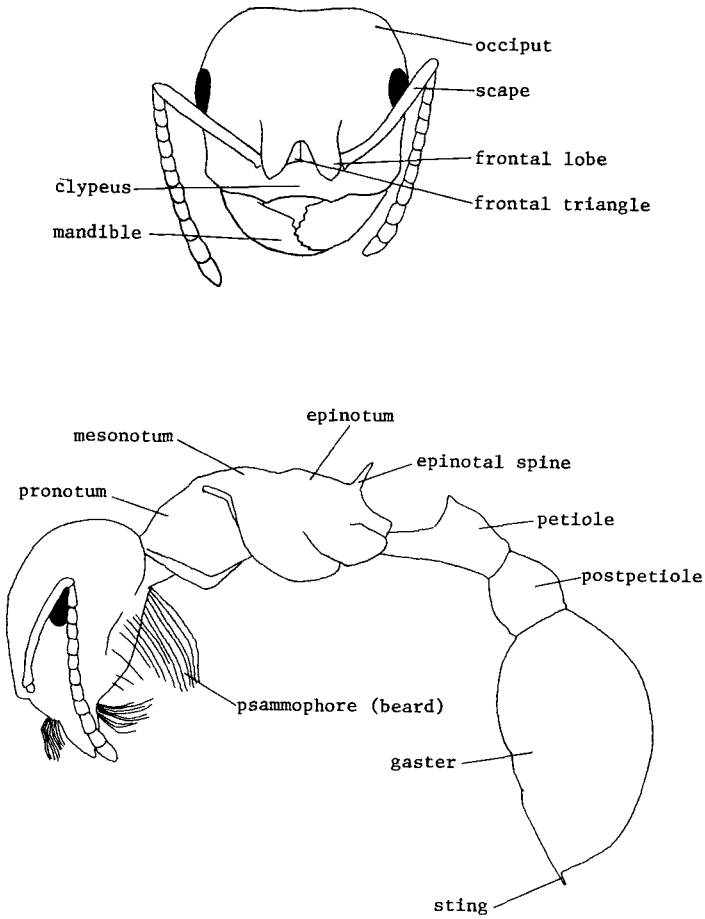
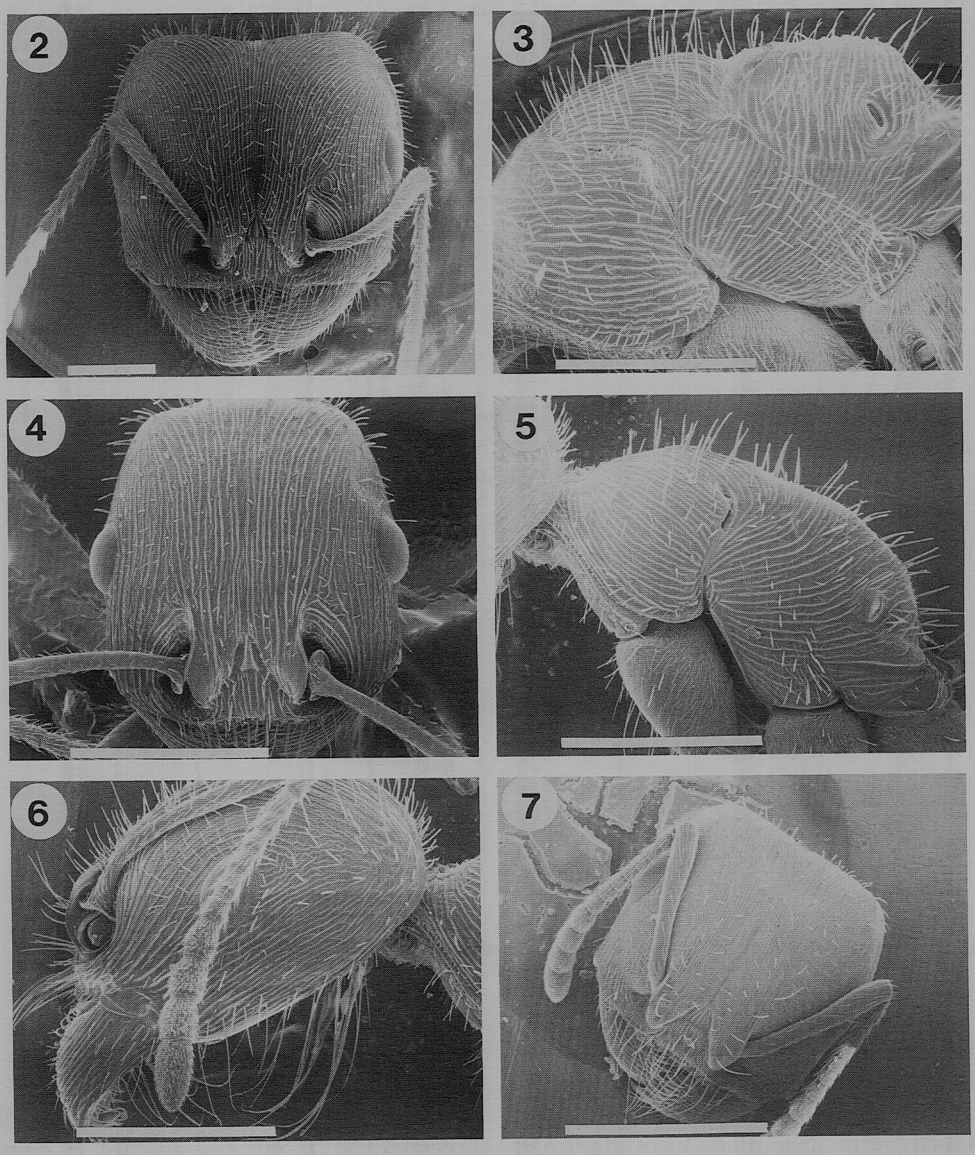


Fig. 1. Gross morphology of *Pogonomyrmex comanche* worker.

have been considered important specific characters, and these spaces are usually described as "smooth" or "punctate." During this study many specimens were identified according to this system using a dissecting microscope, but data obtained from electron micrographs proved this terminology to be inappropriate in every case encountered. For example, the interrugal spaces of *P. montanus* appear strongly punctate under the light microscope which suggests that the surface is covered with punctures or pits. Electron microscopy (450×) revealed tiny rugules that are interconnected in a manner that is best described as "areolate" (Harris 1979). Accordingly, this term is used in place of "punctate" in the following discussions.

Subgenus *Pogonomyrmex*

A. The *badius* complex.—This complex is composed of only one species, *P. badius*. It is the only polymorphic species in North America, the only species to occur east of the Mississippi River, and it is largely allopatric with other congeners over its entire range. The workers are divided into minor, medium, and major size classes, whereas all other species (except for *Pogonomyrmex coarctatus* Mayr of South America) maintain only one worker size class. The large head of the major appears partially bilobed (Fig. 2), and there are no spines on the epinotum (Fig. 3). The scutellum is developed; in all other North American species this

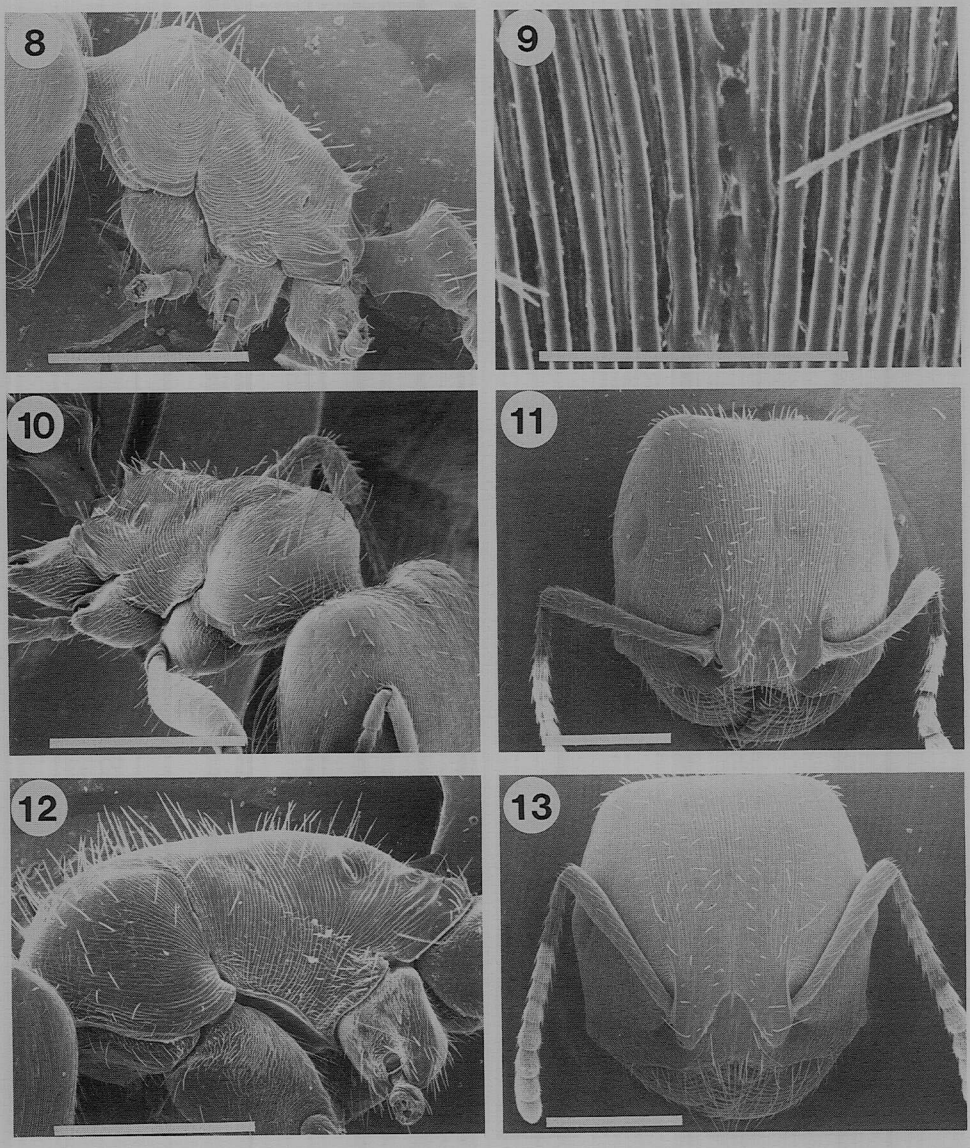


Figs. 2–7. Morphology of *Pogonomyrmex,* scale line = 1.0 mm. 2–6, *P. badius*: 2, Major; head, frontal view. 3, Major; thorax, lateral view. 4, Minor; head, frontal view. 5, Minor; thorax, lateral view. 6, Minor; head, lateral view. 7, *P. desertorum*: head, frontal view.

structure is present only in the reproductive castes.

The minor worker is distinguished by the shape of its head (Fig. 4), which is narrowed behind the eyes. The thorax is less developed (Fig. 5) than that of the major worker, and a lateral view of the head (Fig. 6) reveals the beard for which the genus was named.

B. The *barbatus* complex.—As illustrated by *P. desertorum,* these taxa are distinguished from all other members of the subgenus by a broad head, extended clypeal lobes, straight and parallel cephalic rugae (Fig. 7), and the presence of long, erect hairs on the venter of the petiolar peduncle (Fig. 8). This species is distinguished by the combination of very fine cephalic rugae (Fig. 9), tapering epinotal spines, and a prominent



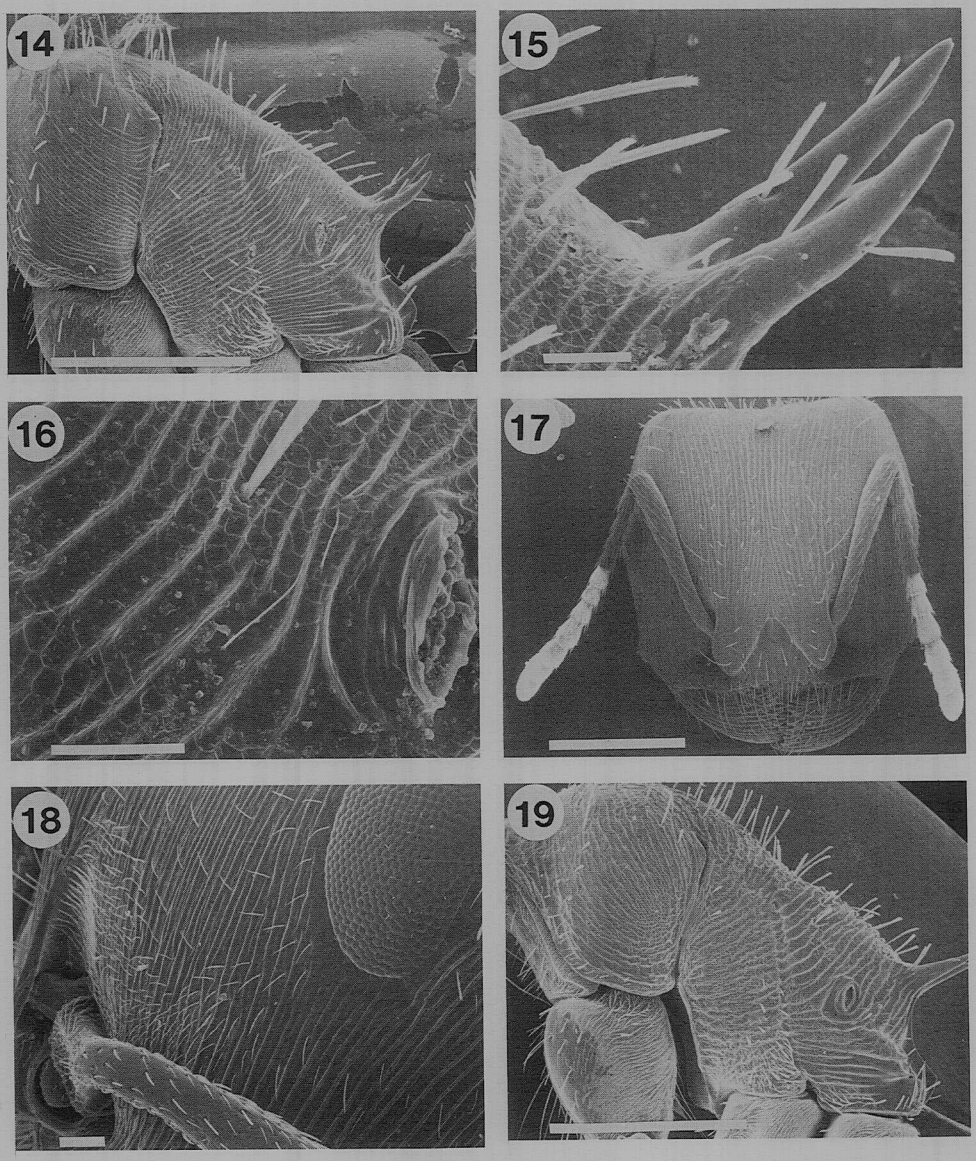
Figs. 8–13. Morphology of *Pogonomyrmex,* scale line for Fig. 9 = 0.1 mm, all others = 1.0 mm. 8–10, *P. desertorum*: 8, Thorax, lateral view. 9, Cephalic rugae, frons. 10, Thorax, dorsolateral view. 11–12, *P. apache*: 11, Head, frontal view. 12, Thorax, lateral view. 13, *P. barbatus*: head, frontal view.

ventral lobe on the petiolar peduncle (Fig. 10).

Pogonomyrmex apache is readily identified by its deeply excised clypeus (Fig. 11). Like *P. desertorum,* this species possesses fine cephalic rugae, but the thorax bears no dorsal spines (Fig. 12).

Pogonomyrmex barbatus is characterized by coarser cephalic rugae (Fig. 13) than the two previous taxa. The head of this species, like other members of the group, is broad. Unlike *P. apache,* this species possesses well-developed epinotal spines (Figs. 14 and 15). A close-up view of the sculpturing and the epinotal spiracle is presented (Fig. 16).

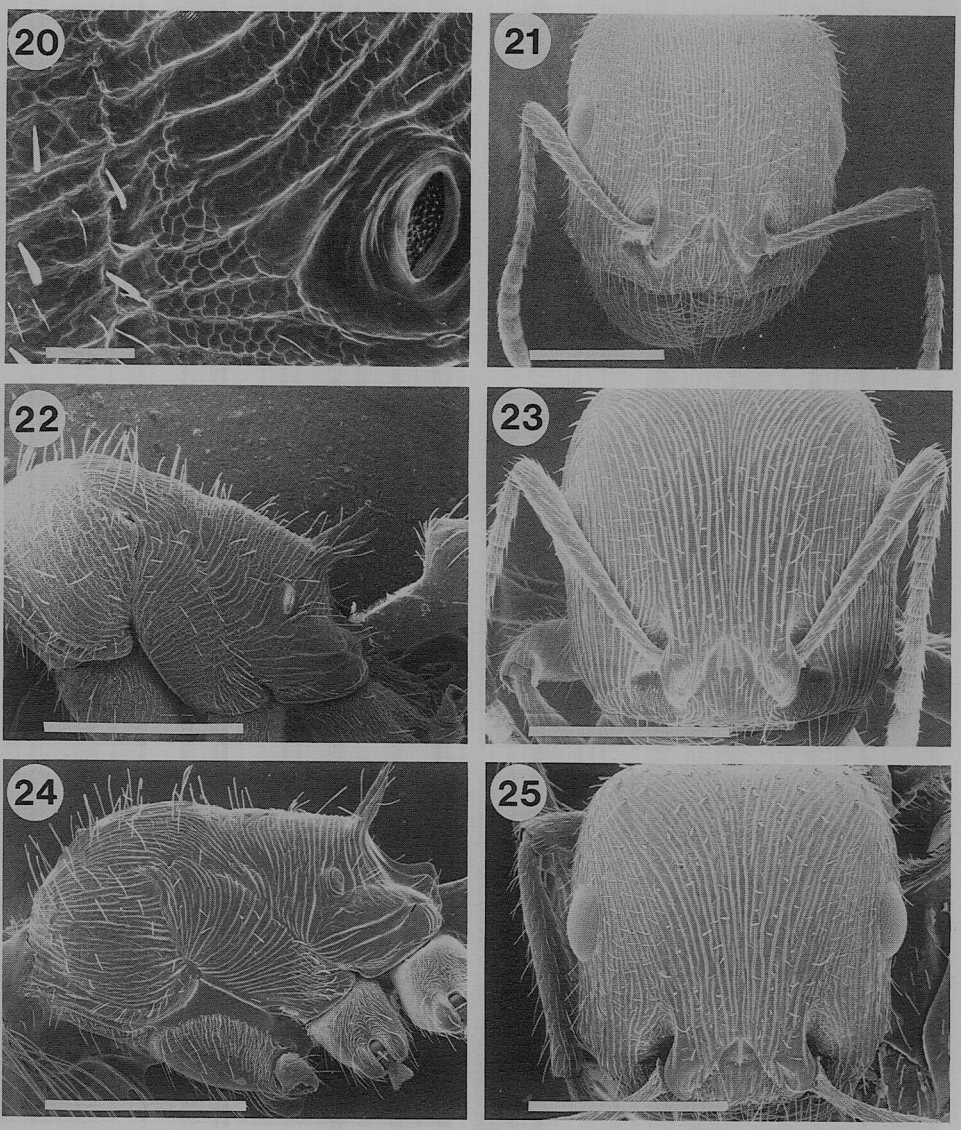
The head of *P. rugosus* bears the coarsest cephalic rugae (termed costulate by Harris, 1979) in the complex (Figs. 17 and 18).



Figs. 14–19. Morphology of *Pogonomyrmex,* scale line for Figs. 15, 16 and 18 = 0.1 mm, all others = 1.0 mm. 14–16, *P. barbatus*: 14, Thorax, lateral view. 15, Epinotal spines. 16, Epinotal spiracle. 17–19, *P. rugosus*: 17, Head, frontal view. 18, Head, lateral view. 19, Thorax, lateral view.

Widely spaced, wavy rugae and epinotal spines are evident on the pronotum and epinotum, respectively (Fig. 19). The rugae are often connected with coarse reticulations (termed porcate by Harris, 1979) (Fig. 20). One of the taxonomic problems presented by the genus is the occurrence of forms that are apparently intermediate between *P. barbatus* and *P. rugosus.* Harris (1979) published photomicrographs of a head and thoracic spiracle region of what he identified as "*Pogonomyrmex barbatus rugosus.*"

C. The *occidentalis* complex.—Members of this complex are characterized by subquadrate heads and more divergent cephalic rugae than those of the *barbatus* com-

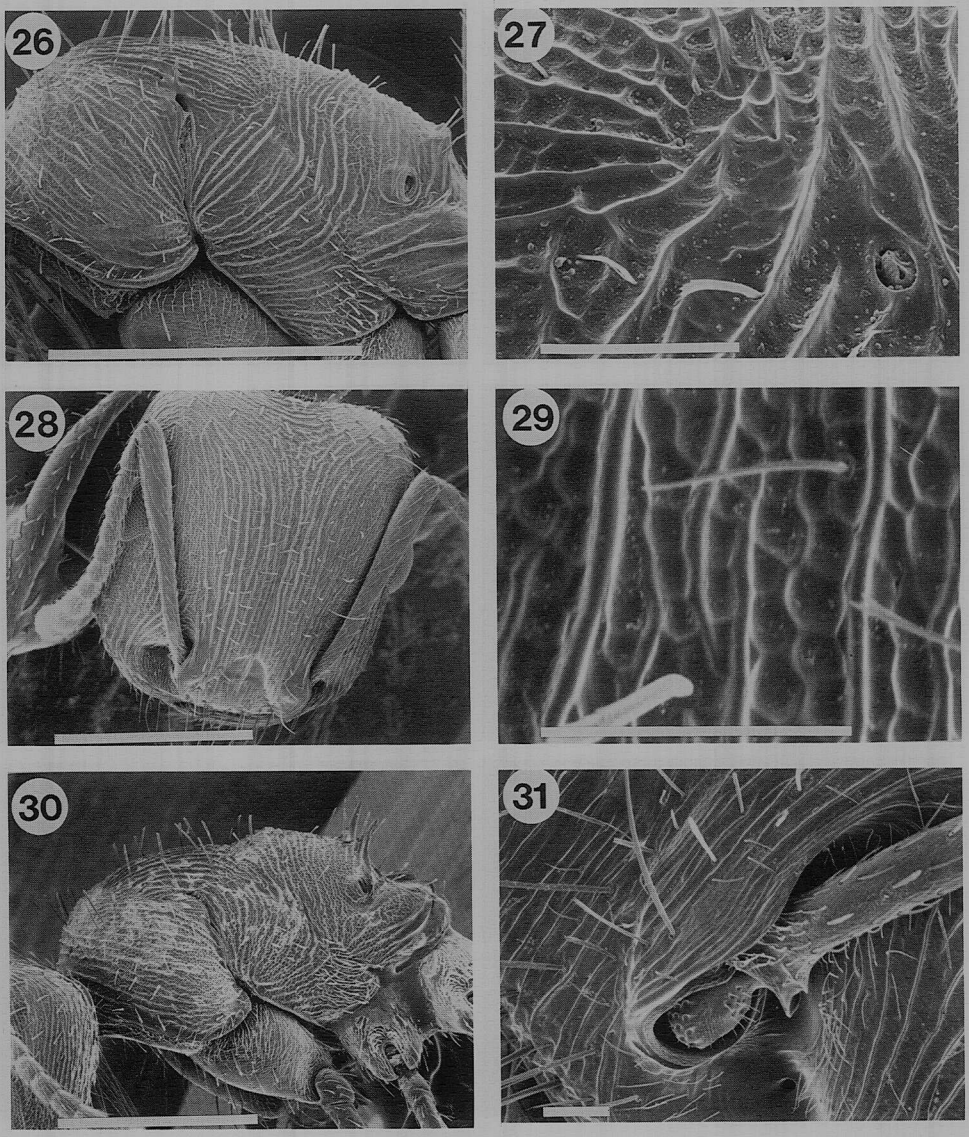


Figs. 20–25. Morphology of *Pogonomyrmex,* scale line for Fig. 20 = 0.1 mm, all others 1.0 mm. 20, *P. rugosus*: epinotal spiracle. 21–22, *P. occidentalis*: 21, Head, frontal view. 22, Thorax, lateral view. 23–24, *P. subnitidus*: 23, Head, frontal view. 24, Thorax, lateral view. 25, *P. brevispinous*: head, frontal view.

plex (Fig. 21). The offset basal mandibular tooth which is diagnostic for *P. occidentalis* is also present (Fig. 21). Epinotal spines are always present in this group and the thoracic dorsum is slightly arched (Fig. 22).

The cephalic interrugal spaces of *P. subnitidus* are not areolate as are those of *P. occidentalis,* but instead are glabrous (Fig. 23). Most of the thoracic interrugal spaces present the same smooth appearance and the spines are well developed (Fig. 24).

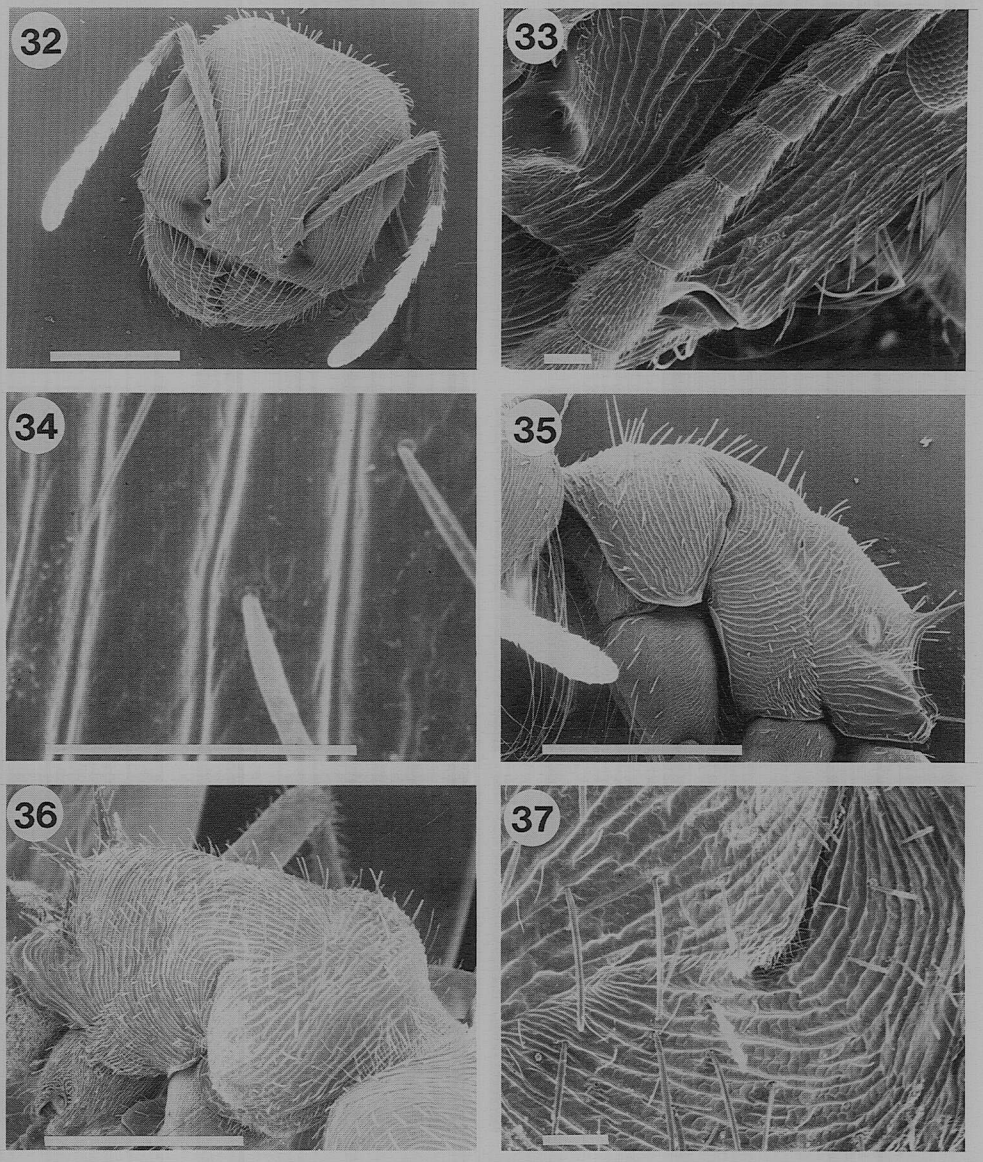
Members of the *occidentalis* complex generally possess wide antennal scape bases (Fig. 25). The cephalic interrugal spaces of *P. brevispinosus* are areolate unlike those of *P. subnitidus,* and the epinotal spines are short (Fig. 26). Areolate thoracic rugae surround the metathoracic spiracle (Fig. 27).



Figs. 26–31. Morphology of *Pogonomyrmex,* scale line for Figs. 27, 29, and 31 = 0.1 mm, all others = 1.0 mm. 26–27, *P. brevispinosus*: 26, Thorax, lateral view. 27, Metathoracic spiracle. 28–30, *P. montanus*: 28, Head, frontal view. 29, Cephalic interrugal spaces. 30, Thorax, lateral view. 31, *P. comanche*: scape base.

MacKay (1980) described a species of harvester ant which he associated with the *occidentalis* complex of Cole. The cephalic interrugal spaces of *P. montanus* are strongly areolate (Figs. 28 and 29). The thorax is highly reticulate and the basal face of the epinotum is elevated (Fig. 30).

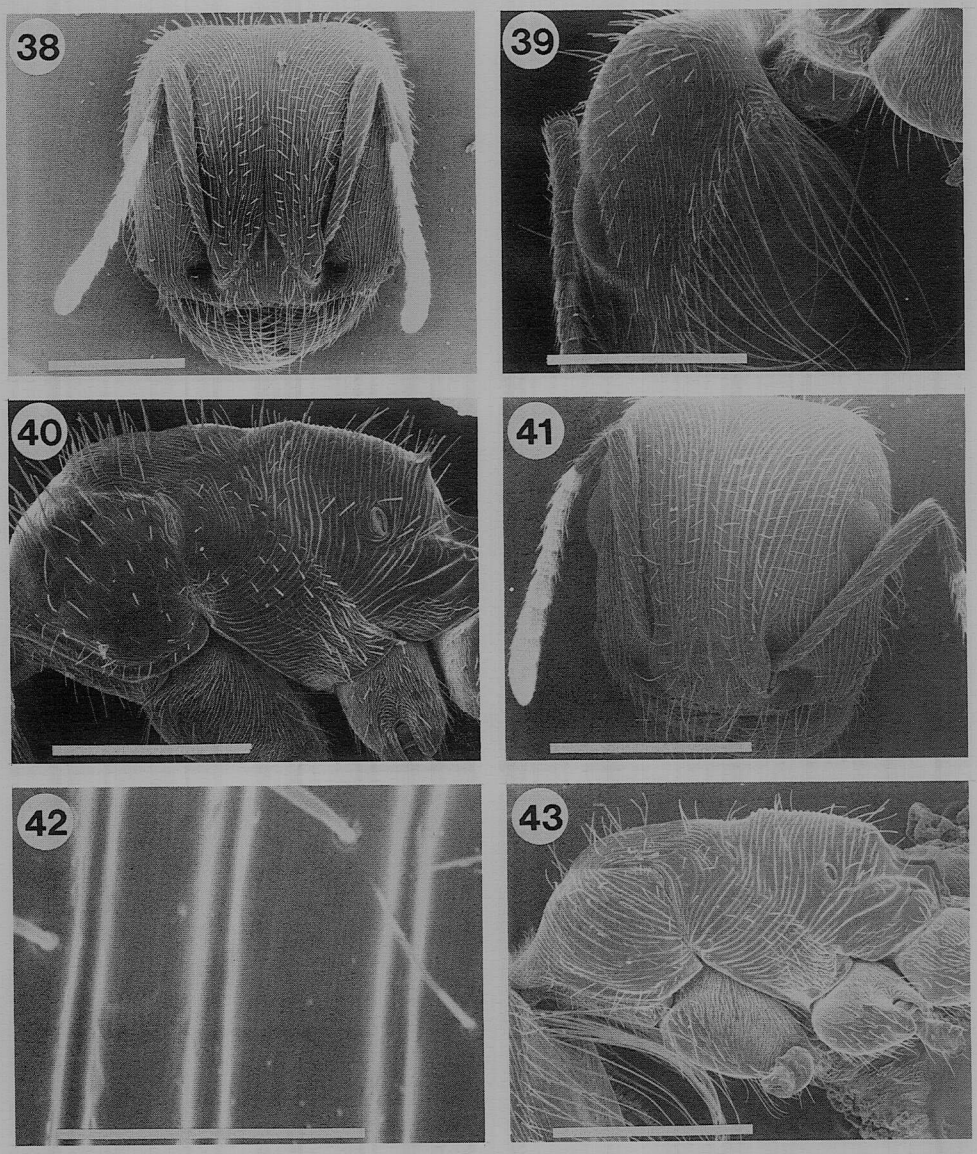
D. The *maricopa* complex.—Representatives of all four members of this group were available for study. The workers may be distinguished from those of the *occidentalis* complex by the weakly enlarged antennal scape base as shown by that of *P. comanche* (Figs. 1 and 31). The cephalic rugae



Figs. 32–37. Morphology of *Pogonomyrmex,* scale line for Figs. 33, 34, and 37 = 0.1 mm, all others = 1.0 mm. 32–37, *P. comanche*: 32, Head, frontal view. 33, Oculomandibular area. 34, Cephalic interrugal spaces. 35, Thorax, lateral view. 36, Thorax, dorsolateral view. 37, Mesothoracic spiracle.

are often coarse (Fig. 32) and may form concentric whorls around the eyes. Cephalic reticulation may be present (Fig. 33), but much of the interrugal surface is smooth (Fig. 34). All members of the *maricopa* complex possess a strongly arched thoracic dorsum, and epinotal spines may be present (Figs. 1 and 35). Both spines (Fig. 36) are present in dorsolateral view, and extremely fine hairs surround the mesothoracic spiracle (Fig. 37).

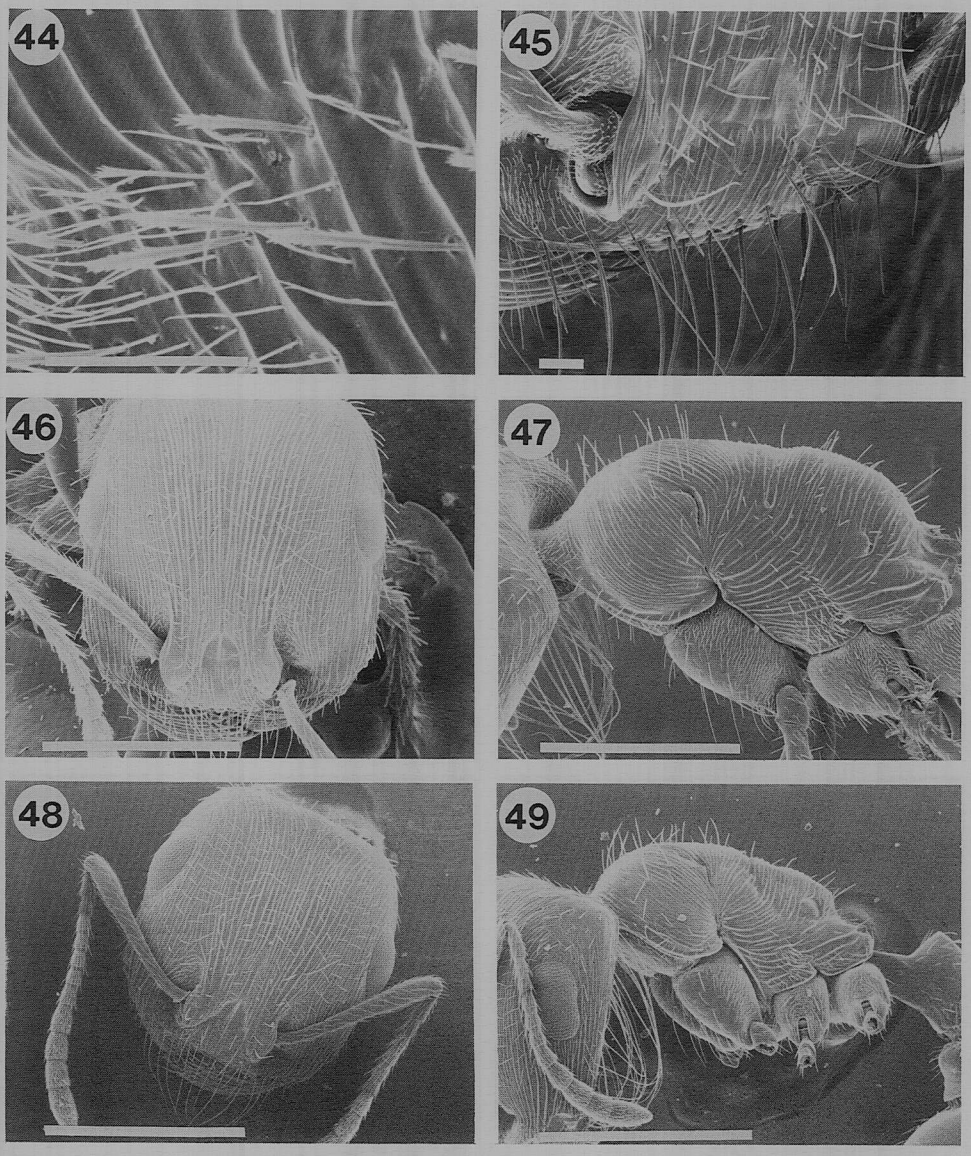
The head of *P. maricopa* is presented in frontal view (Fig. 38). A higher magnifica-



Figs. 38–43. Morphology of *Pogonomyrmex,* scale line for Fig. 42 = 0.1 mm, all others = 1.0 mm. 38–40, *P. maricopa*: 38, Head, frontal view. 39, Psammophore. 40, Thorax, lateral view. 41–43, *P. californicus*: 41, Head, frontal view. 42, Cephalic interrugal spaces. 43, Thorax, lateral view.

tion reveals the psammophore (Fig. 39). The thoracic dorsum is convex (Fig. 40). The specimen illustrated is from a population known as "*maricopa* Variant No. 3" (Cole, 1968). Workers of this variety bear epinotal armature, although the spines may be short.

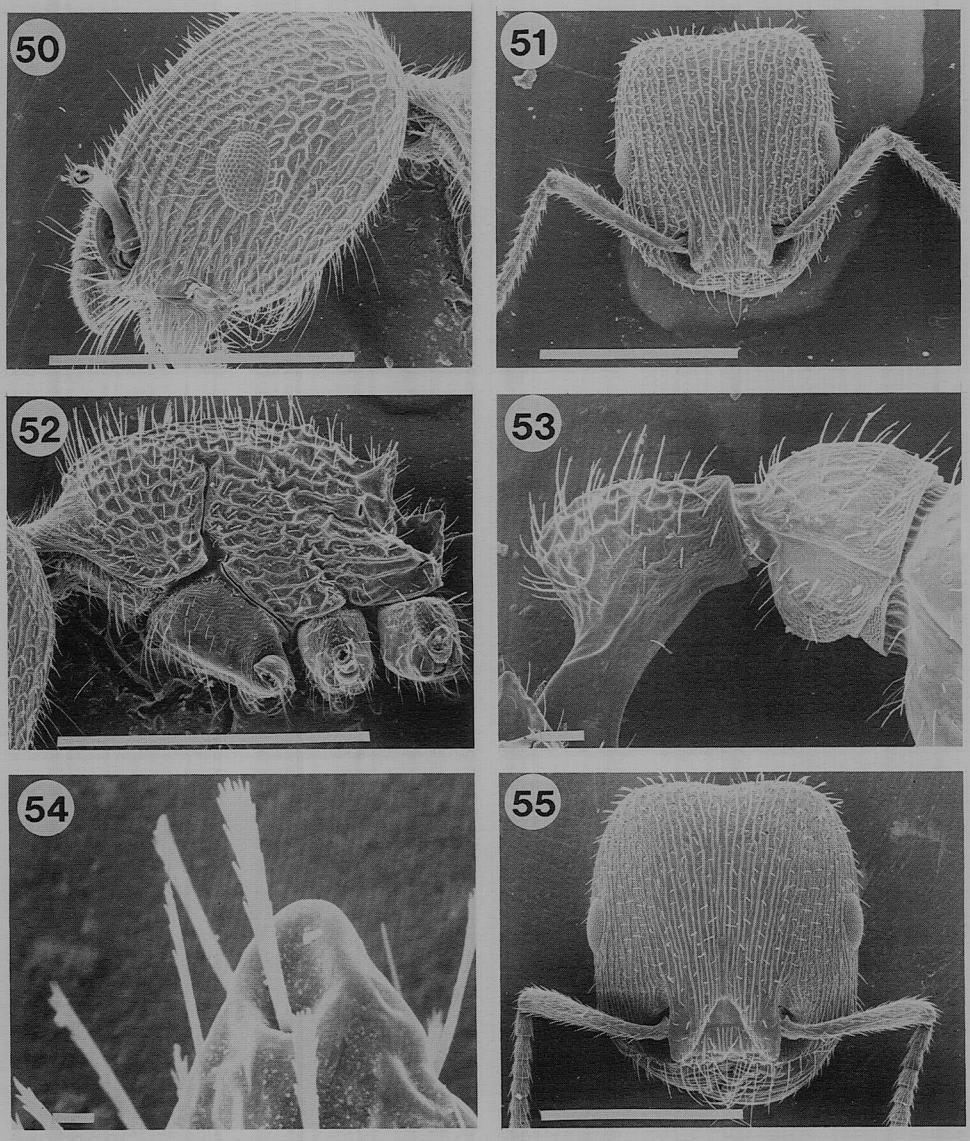
A species often confused with *P. maricopa* is *P. californicus.* However, the cephalic rugae are coarser and reticulation is sparse or absent in the latter species (Figs. 41 and 42). The epinotum is never armed and the epipleura are smooth and costate (Fig. 43). A micrograph of the thorax is also provided by Harris (1979). The mesopleuron bears groups of long, barbed hairs and short, simple hairs (Fig. 44). The shallow frontal triangle is characteristic of both the *occidentalis* and *macricopa* complexes (Fig.



Figs. 44–49. Morphology of *Pogonomyrmex,* scale line for Figs. 44 and 45 = 0.1 mm, all others = 1.0 mm. 44–45, *P. californicus*: 44, Mesopleuron. 45, Frontal triangle. 46–47, *P. californicus* [*estebanius* sensu Pergande]: 46, Head, frontal view. 47, Thorax, lateral view. 48–49, *P. magnacanthus*: 48, Head, frontal view. 49, Thorax, lateral view.

45). Photomicrographs of the head of this species have been published by Scharf (1977: 48) under the name "California Harvester Ant."

Pogonomyrmex californicus estebanius Pergande was synonymized under *P. californicus* by Cole (1968). This subspecific name was given to those taxa presenting a bicolored appearance (the gaster is brown or black, whereas the anterior portion of the ant is red). Cole (1968) noted that eastern populations of *P. californicus* were characterized by finer cephalic rugae and increased "punctation" on the pronotum. A comparison of the previous "typical" *P. californicus* micrographs with those of a *P. californicus*



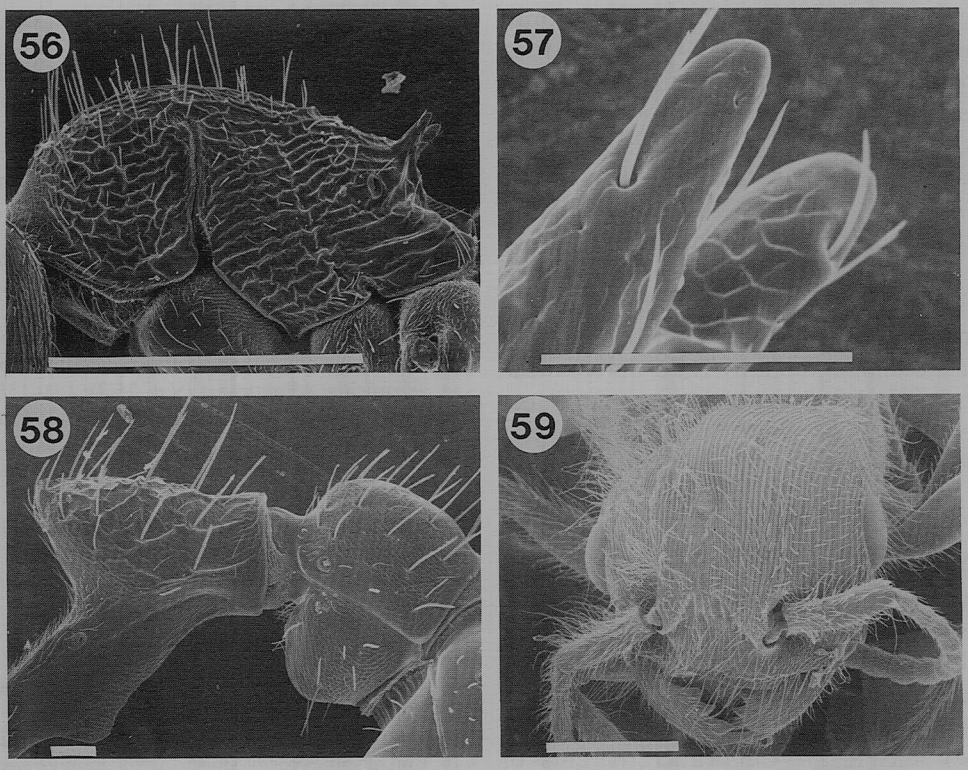
Figs. 50–55. Morphology of *Pogonomyrmex,* scale line for Figs. 53 and 54 = 0.1 mm, all others = 1.0 mm. 50–54, *P. imberbiculus*: 50, Head, lateral view. 51, Head, frontal view. 52, Thorax, lateral view. 53, Pedicel, lateral view. 54, Epinotal spine. 55, *P. huachucanus*: head, frontal view.

[*estebanius* sensu Pergande] specimen collected 197 km southeast of the former (Figs. 46 and 47) supports the contention of Cole (1968), but further study of intermediate samples is needed before the status of the bicolored populations can be accurately determined.

Pogonomyrmex magnacanthus is a small ant which may be readily identified by a pair of exceptionally large compound eyes (Fig. 48). The thorax bears no epinotal spines (Fig. 49).

Subgenus *Ephebomyrmex*

This group is represented in the U.S.A. by three species, one of which was not available for study. *Pogonomyrmex imberbiculus* (Fig. 50) has a relatively undeveloped psam-



Figs. 56–59. Morphology of *Pogonomyrmex,* scale line for Figs. 57 and 58 = 0.1 mm, all others = 1.0 mm. 56–58, *P. huachucanus*: 56, Thorax, lateral view. 57, Epinotal spines. 58, Pedicel, lateral view. 59, *P. occidentalis* (gynandromorph): Head, frontal view.

mophore, one of the characters chosen by Wheeler (1902) to justify the creation of the subgenus. The coarse rugosity and heavy interrugal reticulation shared by all members of the group is also apparent. The compound eyes of these species are placed below the center of the head (Fig. 51). The prominent clypeal angles are diagnostic for *P. imberbiculus* (Fig. 51). Extensive reticulation and coarse rugosity cover the thorax (Fig. 52). A relatively massive postpetiole is present (Fig. 53), and numerous barbed hairs arise from the epinotal spines (Fig. 54).

One of the most problematic species in the genus is *P. huachucanus.* It is often described as intermediate between *Pogonomyrmex* sens. str. and the other two North American *Ephebomyrmex* species. The most obvious such character is the relative size of the ants. *Pogonomyrmex imberbiculus* is the smallest North American species in the genus, whereas *P. huachucanus* is larger, but smaller than almost all members of the nominate subgenus. Rugosity and compound eye placement of *P. huachucanus* appear "intermediate" (Fig. 55). The thorax is not as heavily sculptured (Fig. 56), and the epinotal spines are more slender than those of *P. imberbiculus* (Fig. 57). The less abundant hairs found on these spines are relatively simple, but the postpetiole is proportionately large, as is that of *P. imberbiculus* (Fig. 58).

Sufficient differences between species of *Pogonomyrmex* and *Ephebomyrmex* exist to recognize two genera, as currently done by several other authors. These differences will be further documented in a forthcoming paper on the chromosomes of these species. Some question on the placement of "*E.*" *huachucanus* still remains. The present study and the unpublished data on chromosomes

suggest that this species represents a third group, but we refrain from describing such a group. For the present, it appears best to retain this species in *Ephebomyrmex*. Studies on the third "subgenus" of *Pogonomyrmex* and other species complexes from South America and the West Indies should be instructive, and may aid in an accurate generic placement of "*E.*" *huachucanus*.

The only known bilateral gynandromorph of the genus was described without the use of micrographs by Taber and Francke (1986). The head of that specimen of *P. occidentalis* has a male right side and a predominantly female left side (Fig. 59).

Acknowledgments

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Note: The negatives for Figures 2–59 were provided by the authors and were not photographed by Allen Press, Inc.